flower frequency dependence of pollination (working file)

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1 Introduction

1.1 Introduction (Storyline)

- pollination crucial for most plants (self-incompatible)

- Interspecific and intraspecific competition

- pollinator service shared ressource of coflowering plants

- pollinator attractiveness

- increased forager activity and attractiveness can respond in higher fitness

- response of pollinators to certain variables like density, frequency, traits, etc

- complex multidimensional interactions

- detects bits and peaces to get a greater understanding

- The effect on density is rather well studied

From the proposal:
Frequency-dependence (FD) of survival or reproduction occurs when the relative fitness of a species changes as a function of its frequency in the community. For animal-pollinated plant species, optimal foraging theory predicts that under most circumstances pollinators should favor common flower types over rarer ones (Kunin and Iwasa, 1996) , but so far this has rarely been tested. Most previous studies of frequency-dependent pollination focused on within-species variation in pollination success of different flower color morphs (e.g. **?** , **?**). Other floral traits (e.g. morphology and scent) and interspecific differences in pollination success have rarely been considered in the context of frequency dependence.

According to ecological theory, frequency dependent pollination could have far-ranging consequences for species coexistence and the maintenance of diversity: While negative frequency dependence (i.e., preferential pollination of rare flower types) is thought to increase diversity, positive frequency dependence (higher pollination success for common flower types) tends to reduce diversity in modeling studies (May 1974, but see **?**, **?**).

1.2 Research Questions

1.Does the per-flower pollinator visitation change with the frequency of the flower in a floral community?

2.What kind of a frequency dependent relationship can be found? (linear, positive, negative, saturated, hump shaped, sigmoid)

3.Are there drivers for frequency dependence? (e.g. flower cover, species richness, similarity index, degree of clustering, forager behavior)

In this thesis, I tested the existence of FD within a gradient of frequencies of five flowering plant species in the area of the Jena Experiment. Furthermore, I used an spatially explicit Agent-Based Model (ABM) for the modeling approach. The autonomous agents respond with set foraging behavior rules to changing frequency and clustering values for the two co-flowering plant species.
The results of the model were compared to field data.

2 Methods

2.1 Data Collection

The Jena Experiment:

- N50°55′ E11°35′ ; 130 m a.s.l.

- Established in 2002

- Total Size: 10 hectars

- Arable field for 40 years before experiment started (therefore strongly fertilized)

- Plots are mowed every June and September

- Main experiment has 82 plots, each 20x20m (400m^2)

- Originally sown species mix of 1,2,4,8,16 or 60 species, divided into four blocks (randomized complete block design) along abiotic gradients (mainly soil sand content)

- Part of the Plot is weeded twice a year (not my sampling area)

2.1.1 Choosing Species and Plots

The parts of the plots with continuous weeding were normally very scarce with flowers and had a very low species richness. So I collected the data in the "old invasion plots" (4m x 5.5m , 22m^2) and in the "new invasion plots" (5m x 3.5m, 17.5m^2) with a much higher cover, species richness and diversity. The "old invasion plots" were not weeded since the first seeding in 2002. The "new invasion plots" were not weeded since 2009.

I chose 5 species to observe (Those species were chosen because they were present in min. 5 plots with a differing frequency):

Table 1: Focal Species

Short	Name	German Name	Order	Family	Color
Ono	Onobrychis viciifolia	Saat-Esparsette	Fabales	Fabaceae	pink+white
Lat	Lathyrus pratensis	Wiesen-Platterbse	Fabales	Fabaceae	Yellow
Lot	Lotus corniculatus	Gewöhnliche Hornklee	Fabales	Fabaceae	Yellow
Ger	Geranium pratense	Wiesen-Storchschnabel	Geraniales	Geraniaceae	Purple
TP	Trifolium pratense	Wiesen-Klee	Fabales	Fabaceae	Purple

Because the vegetation changed very quickly (heavy rain and very warm temperatures alternating) I chose max. 7 plots (= 14h) to observe at a time. Every time I finished a session I did a new sampling of all 82 plots of the Jena Experiment to check for suitable plots with focal plant species and their frequencies for the next round. Those observations were randomly distributed over the next days to prevent time dependencies (observation times over the whole day for each plot)

2.1.2 The Sampling

- Observations were made only during good weather conditions (max partly overcast, no rain, max light wind, min. 15 degree)

- Sampling time between 9am and 5pm (there was normally heavy fog and moist in the mornings so I could only start sampling from 10 or even 11)
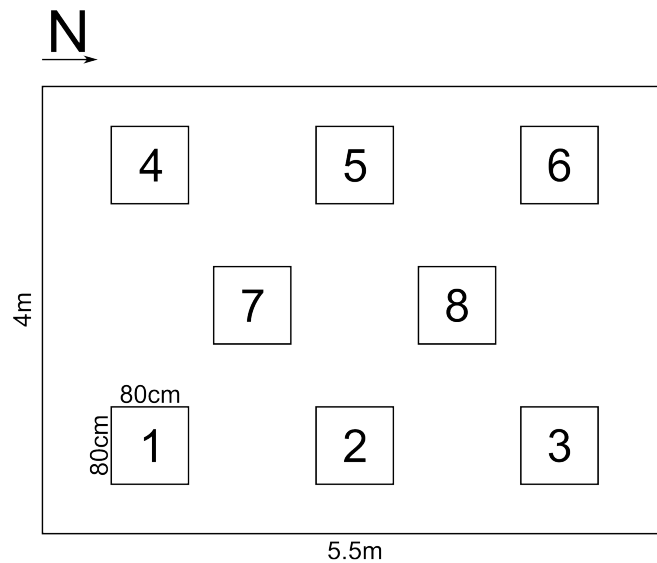
Figure 1: The sampling design within a plot

- Sampling occurred between 20.7. - 12.8.

- Total of 15 sampling days (due to weather conditions)

- The pollinators were divided into bees, bumblebees, hoverflies and "other"

- sampled eight of the 80x80cm patches per plot to get 2h of data per frequency and get a good mean over the plot (flowers were often in clusters and not distributed over the whole plot)

- Patches were distributed as shown in Figure 1

- When the flowers were very unevenly distributed over the Plot (which happened especially at low frequencies) I chose to observe some patches which contained flowers of the chosen species twice

- I normally observed two species at once to save time/get a larger dataset. If there were not too many flowers that was easy feasible. If there were Plots with unevenly distributed flowers as explained above I observed the regular 1-8 patches for the evenly distributed species and additionally doubling patches for the uneven species.

- Eg. Geranium was flowering at all 8 patches, Lotus only in the southern part (patch 1,2,4,5, and 7). I regularly observed all patches 1-8 for Geranium. Because I was missing 3 patches for Lotus I doubled 1, 7 and 5. During this doubling I still kept track of visitors of the Geranium flowers. So in the end my dataset was the following:

  - 8+3 Geranium observations
  - 8 Lotus observations

2.2 Statistical Analysis

2.2.1 The Data

Within the 4 weeks of sampling I got 386 entries, each equivalent to 15min of observation

- Flower visits to the focal species within the patch (divided by pollinator type)

- Flower visits to other flowers except the focal species in the patch (divided by pollinator type)

- Species Richness in the Patch (with names)

- Species Richness in the Plot (with names and quantities)

- Floral Cover in Patch and Plot (own estimation)

- Frequency of the focal species in Patch and Plot

- Count of individual flowers respectively inflorescence of the focal species

- PlotID

- PatchID

- Date/Time

2.2.2 The Analysis

mixed model (lme,lmer,glmer) –¿ glmPQL für p-values
    response variable: Per-Flower visitation rate (summed or by pollinator-subfamily) (poisson)
    fixed: frequency, species richness, flower cover
    random: specID (bin nicht interessiert an der Pflanze sondern an einer allgemeingültigen Aussage, Blüten waren sehr unterschiedlich in der Attraktivität)
    - was ist mit PlotID und PatchID? - ich habe 8 Observations pro Plot, die eigentich irgendwie zusammen gehören... - Similarity-gradient statt einfach SR? - Plot position könnte wichtig sein, näher an beehive oder die Pflanzenzusammensetzung - Habe auch Daten zur Visitation Rate aller anderen Arten, ralative Vr interessant?
    Backwards selection with AIC

2.3 The Model

2.3.1 About ABMs

Agent-Based Model (ABM, also known as Individual-Based Model IBM) Every pollinator (bee-agent) behaves independently after the given behavior rules Very good for testing behavior change with changing environmental conditions (eg. nectar reward or flower quantity)

NetLogo (Wilensky, 1999) is a simple programming environment for ABMs and connectable with R through the RNetLogo-Package.

Agent-based models get more attractive throughout the modeling community of various research areas. Foraging models also grew in number over the last years.

Faruq et al. (2013) compared the foraging success while applying different color wavelengths.

Dornhaus et al. (2006) looked at the benefits of a recruitment system and colony sizes.

Bukovac et al. (2013) simulated the difference between the parallel visual scan of honey bees and the serial visual scan of bumble bees to for the ability to avoid distractions during foraging.

Dyer et al. (2014) trained honey bees in a lab experiment to fine color discrimination to check for their flexibility to change when the reward changes between flower types. Afterwards, Dyer et al. (2014) confirmed the findings with a ABM.

The ABM of Hanoteaux et al. (2013) showed reproduction success of plants in a combination of spatial arrangement and relative frequency of flowers with unequal attraction to the pollinator.

2.3.2 The Environment

In NetLogo, the "world" contains a spatial grid with a set number of cells calles patches. Agents move freely over the patches after their behavior rules. Patches and agents can both have own properties and can interact with each other. The meadow has 100x100grid cells with horizontally and vertically wrapping to avoid edge effects. Every grid cell can either contain a single flower of one of the two species or grass. Flowers of two species are randomly distributed over the meadow. Every flower contains 1Joule of floral reward in the beginning of each simulation run. The bee-agents are also randomly distributed over the modeling environment, no hive is assigned. Bee-agents start without a fixed preference for a flower type but just pick the closest one when the simulation starts.

2.3.3 Assumptions

- All pollinators are identical

- All flowers types are equal (also in terms of reward regrowth, handling times and attractiveness to the pollinator)

- Pollinators behave under the theory of flower constancy

  - Change when search is unsuccessful
  - Chance when species is not rewarding any more

- All bees have a memory for recently visited flowers and gained reward

- Pollinators follow the "correlated random walk" if no target is assigned

- Energetic costs are ignored

- The reward is completely emptied by each visit and can be renewed over time

- Pollinators do not communicate

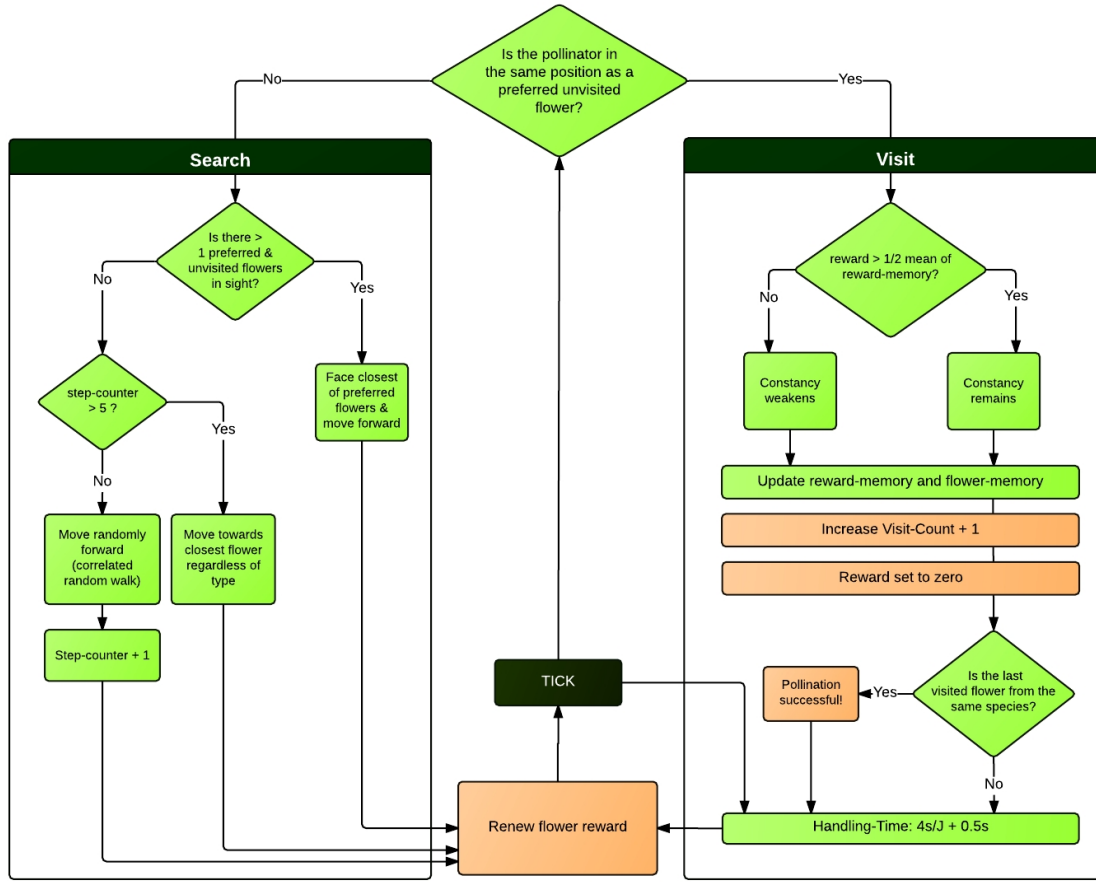- Pollinators only use one trait to choose flower (visual)

Figure 2: Flowchart describing the behavior rules for the bee-agents within the Agent-Based Model. Every bee-agent can either search for a preferred flower or visit one. While searching, a bee-agent can remember the location of the last four visited flowers to avoid double-encountering. If there is no flower in sight after 5 seconds of CRW it will encounter the next available flower despite its type. When a bee-agent visits a flower it takes all reward within a reward-dependent handling time and compares the amount with its memory. If the reward is low, the agent is more likely to visit the other flower type next time. Successful pollination takes place if the last visited flower was from the same flower type.

- Pollinators do not have a limit of gained rewards

- Pollinators are randomly distributed, no hive is assigned (no central place foragers)

2.3.4 Behavior rules

All bee-agents act independently from each other after given foraging behavior shown in Figure 2. The bee-agent can either search for a flower or visit one. Every tick in NetLogo equals one second.

The behavior of the bee-agents is strongly influences by the theory of flower constancy (e.g. Bobisud and Neuhaus, 1975; Chittka et al., 1997; Thomson, 1981; Chittka et al., 1999; Goulson, 1994, 1999). Bee-agents will always be in favor of one of the two flowering species and will not visit the other flower type. This preference can change due to lack of searching success and a series of low rewards of the preferred flower (Chittka et al., 1997). Pollinators avoid recently visited flowers (Goulson, 1999). Every bee-agent is equipped with a memory

to remember the location of the last 4 already visited flowers (Goulson, 2000).

If there is any preferred and unvisited flower in sight it will turn toward it and move towards the flower. If there is no unvisited, preferred flower in sight the bee agent continues searching.

Previous research on the speed of foraging pollinators by Essenberg (2012) and Kunin (1991) (see Kunin and Iwasa 1996) gave 0.1m/sec as benchmark. Sequentially, bee-agents can move as fast as 1 grid cell per tick in this model.

The vision of pollinators was studied in various experiments using a Y-maze apparatus (Dyer et al., 2008; Wertlen et al., 2008; Ne'eman and Kevan, 2001). In this model, every bee-agent can detect flowers from a distance of 0.7m with an equivalent of 6 grid cells. Also, it is reduced to a 180° cone-shaped field to the front of the agent.

Pollinators tend to keep their direction while foraging (Waddington, 1980). In the model, I used a correlated random walk (CRW) to achieve a relatively natural movement (Bartumeus et al., 2005; Codling et al., 2008; Pyke and Cartar, 1992; Viswanathan et al., 2008).

Empirical studies have shown a higher probability to abandon the original flower preference the longer the search remains unsuccessful (Chittka et al., 1997). Therefore will the bee-agent forage on the next available flower regardless its species after 5 seconds (= 5 ticks) of CRW without finding any preferred and unvisited flower.

When a bee-agent encounters a preferred and unvisited flower it takes up all its reward in a reward-dependent handling time. The maximal reward a flower can contain is 1J and refills each tick by a linear function. A bee-agent requires 4 seconds to extract one Joule of reward plus an additionally reward-independent handling time of 0.5 seconds (**?** in Kunin and Iwasa 1996).

The reward taken is stored in the agent-own reward-memory. Every agent can remember the last four receives rewards. When visiting a flower, the bee-agent compares this memory with the current reward quantity. If the reward is less than half the average in the memory, the likelihood to abandon flower constancy and visit another flower type next increases (Chittka et al., 1997; **?**).

For simplicity reasons, the pollen carryover rate for successful pollination is just one visit. If the last visited flower was the same species, successful pollination takes place (Campbell 1986; Benadi et al. 2012 but see Montgomery 2009).

After full collection of the reward, the bee-agent updates its flower-memory and its reward-memory and continues foraging. Each visit and successful pollination is recorded for later analysis.

Table 2: Parameter values

Parameter	Description	NetLogo-Type	Type	Value	Reference
area	"world" in NetLogo, number of grid-cells		integer	100x100	
patch-size	Size one grid-cell in NetLogo. Can be either a flower or grass		float	0.1m²	
tick	One time-unit in NetLogo		integer	1s	
number-bees	Initial number of pollinators in the model	global	integer		0.0004 - 1 bee/m² (Essenberg, 2012)
flower-cover	Proportion of grid cells containing a flower	global	integer		
frequency	Proportion of flowers which are species A feq(B) = 100 - freq(A)	global	integer		
search-speed	Distance a pollinator can move per tick	bees-own	integer	0.1m/sec	(Kunin, 1991) in (Kunin and Iwasa, 1996) 0.09-0.17 (Essenberg, 2012)
stdev-angle	Standard deviation for the normal distribution used in the CRW	global	integer	65	Waddington 1980
flightsteps-until-change	seconds of unsuccessful search before the constancy changes	bees-own	integer	5s (= 5 ticks)	Chittka et al. 1997
length-memory	How many flowers can a bee remember to avoid double-visiting.	bees-own	integer	4	Goulson 2000, see Goulson 1999 for review
view	Value for the radius of grid-cells a pollinator can see (cone-view of 180°)	bees-own	integer	0.7m (= 6 grid-cells)	(Dyer et al., 2008; Wertlen et al., 2008)
reward-function	How fast the reward is renew per second	flowers-own	float	0.00004 J/s	Nè'eman and Kevan 2001
handling-time	The time a pollinator needs for exploiting the floral reward	bees-own	integer	reward * 4s + 0.5s	? in Kunin and Iwasa 1996
reward	Reward in Joule the flower has to offer. Exploited with each visit, renewed over time	flowers-own	float	reward(max) = 1J	Kunin 1991 in Kunin and Iwasa 1996
pollen carry-over rate	The max. number of visits within a successful pollination is possible	flowers-own	integer	1	see Goulson 1999 for review
flower-memory	A list of flower-locations	bees-own	string		
reward-memory	A list of the last rewards	bees-own	string		
change-prob	Probability to change the preferred flower type. Increases with low reward	bees-own	float		
spec-last-visit	The species of the last visited flower (for pollination)	bees-own	boolean		
pollination-count	Counts the number of successful pollination	flowers-own	integer		
choice	Current flower choice for the pollinator (for constancy)	bees-own	boolean		
array	Array of all suitable flowers (referred, non-visited) flowers in sight of the pollinator	bees-own	Array		
species	Determines the species of the flower	flowers-own	boolean		
end	Number of time steps until the model ends		integer		

Results
….das kommt dann noch irgendwann :)

3 Discussion

4 Conclusions

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